Distinct computational principles govern multisensory integration in primary sensory and association cortices

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Report

Current Biology

Distinct Computational Principles Govern Multisensory Integration in Primary Sensory and Association Cortices

Highlights

- Multisensory interactions differ computationally across the cortical hierarchy
- In visual cortex, spatial disparity controlled the influence of auditory signals
- In parietal cortex, spatial disparity determined the effect of task-irrelevant signals
- Only parietal cortices weighted signals by their reliability and task relevance

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In Brief

Rohe and Noppeney show that multisensory interactions are pervasive but governed by distinct computational principles across the cortical hierarchy. Critically, only parietal cortices integrated signals weighted by their bottom-up sensory reliabilities and top-down task relevance into multisensory spatial priority maps.

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Distinct Computational Principles Govern Multisensory Integration in Primary Sensory and Association Cortices

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SUMMARY

Human observers typically integrate sensory signals in a statistically optimal fashion into a coherent percept by weighting them in proportion to their reliabilities [1–4]. An emerging debate in neuroscience is to which extent multisensory integration emerges already in primary sensory areas or is deferred to higher-order association areas [5–9]. This fMRI study used multivariate pattern decoding to characterize the computational principles that define how auditory and visual signals are integrated into spatial representations across the cortical hierarchy. Our results reveal small multisensory influences that were limited to a spatial window of integration in primary sensory areas. By contrast, parietal cortices integrated signals weighted by their sensory reliabilities and task relevance in line with behavioral performance and principles of statistical optimality. Intriguingly, audiovisual integration in parietal cortices was attenuated for large spatial disparities when signals were unlikely to originate from a common source. Our results demonstrate that multisensory interactions in primary and association cortices are governed by distinct computational principles. In primary visual cortices, spatial disparity controlled the influence of *non-visual signals* on the formation of spatial representations, whereas in parietal cortices, it determined the influence of *task-irrelevant signals*. Critically, only parietal cortices integrated signals weighted by their bottom-up reliabilities and top-down task relevance into multisensory spatial priority maps to guide spatial orienting.

RESULTS

Our senses are exposed to a constant influx of signals. To make sense of this cacophony, the brain needs to solve two computational challenges: first, it needs to determine which signals emanate from a common source based on them co-occurring in time (e.g., temporal synchrony) and space (e.g., spatial disparity) [4, 10, 11]. Second, it needs to integrate signals from a common source into a statistically optimal percept by weighting them in proportion to their reliabilities [1–3]. To determine the functional relevance and computational principles that govern multisensory interactions across the cortical hierarchy, we presented five participants with synchronous audiovisual spatial signals that varied in their spatial disparity and visual reliability (Figures 1A and 1B). On each trial, participants reported their perceived location of the auditory or visual signal. The study was approved by the human research review committee of the University of Tübingen.

Combining psychophysics and multivariate fMRI pattern decoding, we characterized how human observers integrate auditory and visual signals into spatial representations in terms of the audiovisual weight index w_{AV} that quantifies the influence of the true auditory and visual locations on (1) the perceived/reported auditory and visual spatial estimates (i.e., participants' behavioral localization responses; Figure 1C) and (2) the spatial estimates decoded from regions of interest along the auditory [12] and visual [13] dorsal processing hierarchy (Figure 2). This audiovisual weight index ranges from pure visual (90°) to pure auditory (0°) influence. We performed the statistics on the behavioral and neural audiovisual weight indices using a two (auditory versus visual report) × two (high versus low visual reliability) × two (large versus small spatial disparity) factorial design based on circular statistics [14].

Behavioral Results

Our results demonstrate that participants integrated auditory and visual signals weighted by their reliabilities and task relevance (see Table 1; see Figure S1 for histograms of reported signal locations across all conditions). The relative influence of the visual signal on participants' perceived location was greater for high relative to low visual reliability (main effect of visual reliability: $p < 0.001$; permutation testing of a likelihood ratio test statistic). Moreover, it was greater when the location of the visual signal needed to be reported than when the location of the auditory signal needed to be reported (main effect of task relevance: $p < 0.001$). Thus, participants flexibly adjusted the weights according to the task-relevant sensory modality. As a consequence, they reported different auditory and visual locations for identical audiovisual signals. Critically, this difference significantly increased for large (>6.6°) relative to small (≤6.6°) spatial disparities. In other words, audiovisual

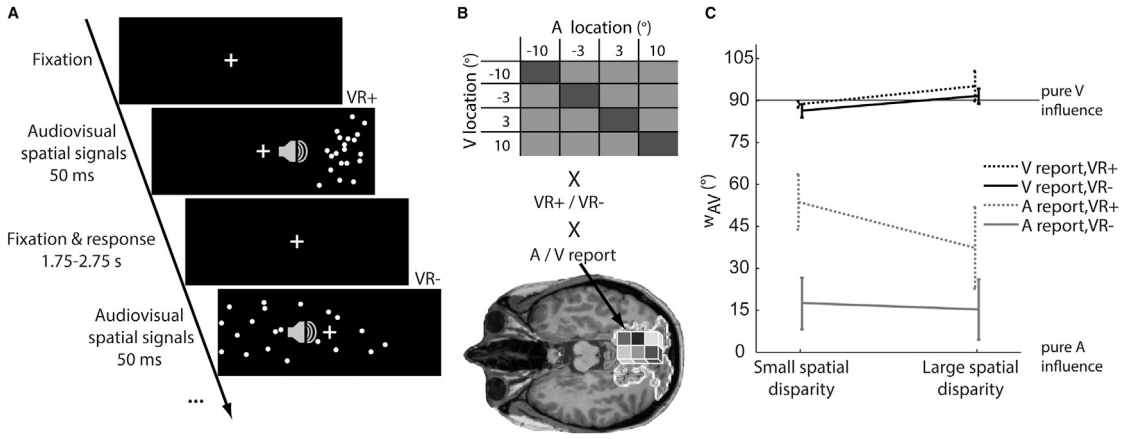

Figure 1. Example Trial, Experimental Design, and Behavioral Data

(A) In a ventriloquist paradigm, participants were presented with synchronous audiovisual signals originating from four possible locations along the azimuth. The visual signal was a cloud of white dots. The auditory signal was a brief burst of white noise. Participants localized either the auditory or the visual signal (n.b. for illustrational purposes the visual angles of the cloud have been scaled in a non-uniform fashion in this scheme).

(B) The four-factorial experimental design manipulated (1) the location of the visual (V) signal (−10°, −3.3°, 3.3°, and 10°), (2) the location of the auditory (A) signal (−10°, −3.3°, 3.3°, and 10°), (3) the reliability of the visual signal (high [VR+] versus low [VR−] reliability as defined by the spread of the visual cloud), and (4) task relevance (auditory versus visual report). Using fMRI, we measured activation patterns to audiovisual signals of all experimental conditions from voxels of regions along the auditory and visual spatial-processing hierarchies.

(C) Behavioral results: audiovisual weight index w_{AV} (across-participants circular mean and double-bootstrapped 68% confidence interval; n = 5) was computed as the angle between the auditory and visual regression coefficients. Audiovisual weight index w_{AV} as a function of audiovisual spatial disparity (small [≤6.6°] versus large [>6.6°]), task relevance (auditory versus visual report), and visual reliability (high [VR+] versus low [VR−]) are shown. For a purely visual influence, w_{AV} is 90°. For a purely auditory influence, it is 0°.

See also Figure S1.

integration broke down when auditory and visual signals were far apart and more likely to be caused by independent sources (i.e., a significant interaction between task relevance and spatial disparity; p = 0.015).

fMRI Decoding across the Cortical Hierarchy

To characterize how auditory and visual signals were integrated into spatial representations at the neural level, we combined fMRI with multivariate pattern decoding. Based on a support-vector regression model trained on audiovisual spatially congruent trials, we decoded a brain area's spatial estimate of spatially disparate audiovisual signals. First, we ensured that we could decode the spatial estimate for congruent trials significantly better than chance in all eight regions of interest (Table S1). Using the same analysis approach as for behavioral localization responses, we then investigated how the neural audiovisual weight w_{AV} index was affected by visual reliability, task-relevant sensory modality, and spatial disparity (Figures 2A–2D). As the two (auditory versus visual report) × two (high versus low visual reliability) × two (large versus small spatial disparity) repeated-measures analysis did not reveal a significant three-way interaction (Table 1), Figure 2 presents the neural audiovisual weights separately as a function of visual reliability, task relevance, and spatial disparity (Figures 2A–2C) and of both task relevance and spatial disparity (Figure 2D).

Effect of Sensory Reliability on Audiovisual Integration

First, we asked which regions integrate auditory and visual signals weighted by their reliability as expected from principles of statistical optimality [1–3] and participants' behavioral localization responses (Figure 2A). Surprisingly, visual reliability did not significantly influence audiovisual weighting in lower visual or auditory areas. Only higher parietal cortices (IPS0–IPS4) were governed by the classical reliability-driven reweighting with more weight being given to the auditory signal when the visual signal was unreliable. Whereas IPS0–4 mainly represented the location of the visual signal for high visual reliability (i.e., the audiovisual weight index was approximately 90°), its spatial estimate shifted toward the location of the concurrent auditory signal for low visual reliability.

Effect of Task Relevance on Audiovisual Integration and Its Interaction with Spatial Disparity

Next, we asked where auditory and visual signals were integrated into spatial representations weighted by their task relevance (Figure 2B). Whereas we found a marginally significant main effect of task relevance (i.e., visual versus auditory report) on the audiovisual weight index already in higher-order auditory areas (hA) encompassing the belt and the planum temporale, the effect emerged predominantly in higher-order association areas such as IPS0–4 (cf. Table 1). In these areas, the visual signal exerted a stronger influence on the decoded location during visual than auditory report. Thus, both planum temporale and IPS0–4 formed different spatial estimates for identical audiovisual stimuli depending on which sensory modality was attended and reported.

Importantly, the difference between spatial estimates for auditory and visual report was further increased in IPS3–4, when the spatial disparity between auditory and visual signals was large (i.e., significant interaction between task relevance and spatial

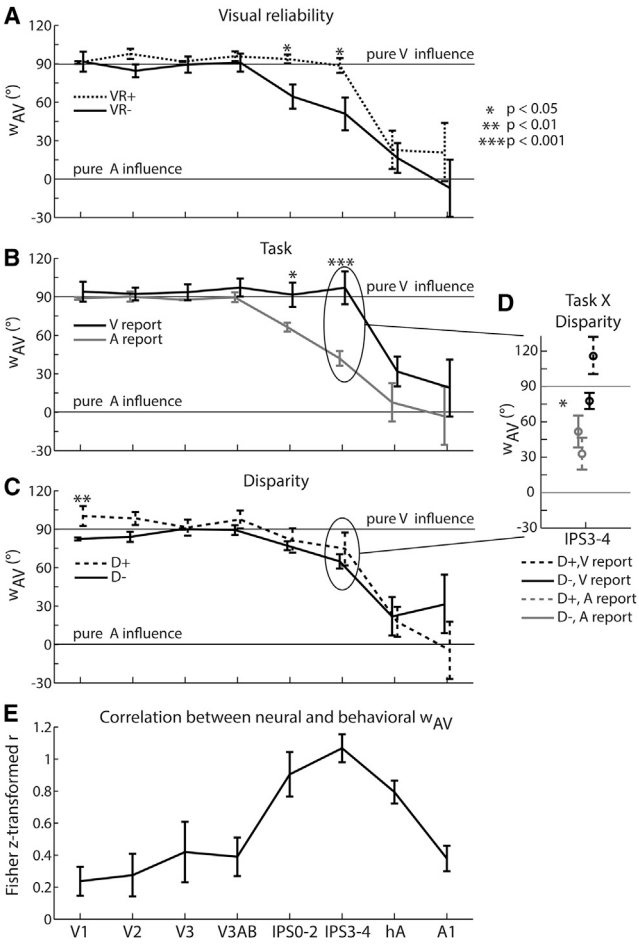

Figure 2. fMRI Results

Audiovisual weight index as a function of visual reliability, task relevance, and disparity and its correlation with the corresponding behavioral weight index in the regions of interest. Audiovisual weight index w_{AV} (across-participants circular mean and double-bootstrapped 68% confidence interval; n = 5) was computed as the angle between the auditory and visual regression coefficients. For a purely visual region, w_{AV} is 90°. For a purely auditory region, it is 0°. Asterisks indicate the statistical significance of effects on w_{AV} derived from a circular log-likelihood ratio statistic.

(A) Audiovisual weight index w_{AV} as a function of visual reliability (high [VR+] versus low [VR−]).

(B) Audiovisual weight index w_{AV} as a function of task relevance (auditory [A] versus visual [V] report).

(C) Audiovisual weight index w_{AV} as a function of audiovisual spatial disparity (small [≤6.6°; D−] versus large [>6.6°; D+]).

(D) Audiovisual weight index w_{AV} in IPS3–4 as a function of task relevance and disparity.

(E) Circular-circular correlation (across-participants mean after Fisher z-transformation ± SEM; n = 5) between the neural weight index w_{AV} and the equivalent behavioral weight index in the regions of interest.

See also Figure S2 and Tables S1 and S2.

disparity; cf. Table 1). In other words, when audiovisual spatial disparity was large and signals were unlikely to emanate from a common event, audiovisual interactions broke down and IPS3–4 predominantly represented the location of the task-relevant signal. Thus, spatial disparity controlled the influence of the task-irrelevant signal on the spatial estimate in IPS3–4.

Effect of Spatial Disparity on Audiovisual Integration

In contrast to the interaction between task relevance and spatial disparity that was found in parietal areas, we observed a main effect of spatial disparity in low-level visual areas V1 and, marginally significant, in V2 (cf. solid lines are below dotted lines in V1 and V2; Figure 2C; Table 1). Only for small spatial disparities auditory signals exerted an "attractive" influence on the spatial representations decoded from low-level visual areas (cf. solid lines below 90° in V1; p = 0.094 in a one-sample permutation test in Figure 2C). Likewise, we observed a limited but significant attractive influence of visual signals on spatial representations decoded from auditory areas for small spatial disparities (solid lines above 0° in A1 in Figure 2C; p = 0.032 for unidirectional hypothesis in a one-sample permutation test). These results suggest that integration in low-level sensory areas depends on auditory and visual signals co-occurring within a spatial window [15]. In short, spatial disparity controls the influence of the non-preferred sensory signals on the spatial estimates in low-level sensory areas.

Note, however, that spatial disparity was inherently correlated with the eccentricity of the audiovisual signals by virtue of the factorial and spatially balanced nature of our design. Whereas signals were presented para-foveally or peripherally for small-disparity trials, they were presented in the periphery for large-disparity trials.

Interaction between Spatial Disparity and Visual Reliability

For completeness, we also observed an interaction between reliability and spatial disparity in V3AB. This interaction results from a larger spatial window of integration for less-reliable sensory signals (see [16]). Basically, it is easier to determine that two signals come from different sources when the visual input is reliable.

Relation of Neural and Behavioral Weight Indices of Audiovisual Spatial Integration

Finally, we asked how and where along the cortical hierarchies the neural audiovisual weights were related with the behavioral audiovisual weights. Hence, we computed the correlation between the neural and behavioral weight indices for each of the regions of interest. The correlation coefficient increased along the visual processing hierarchy culminating in IPS3–4 (Figure 2E). Likewise, in the auditory system, the correlation between neural and behavioral weights was enhanced in higher-order auditory areas relative to primary auditory cortex.

To further investigate which region predominantly drove participants' perceptual localization responses, we decoded the reported signal location from fMRI activation patterns while accounting for the physical signal location and visual reliability. IPS3–4 showed the greatest and selectively significant correlation coefficient between true and decoded reported locations (Table S1).

Collectively, these results suggest that audiovisual integration processes in higher-order visual (in particular IPS3–4) and auditory areas are closely related to participants' trial-by-trial perceived stimulus location.

Controlling for Eye Movements and Hemifield of Signals as Potential Confounds

To address potential concerns that our decoding results may be confounded by eye movements, we performed a series of

Table 1. Statistical Significance of Main and Interaction Effects of the Factors Visual Reliability, Task Relevance, and Spatial Disparity for the Behavioral and Neural Audiovisual Weight Index w_{AV}

	VR p	TR p	S p	VR × TR p	VR × S p	TR × S p	VR × TR × S p
Behavior	<0.001*	<0.001*	0.607	0.002*	0.186	0.015*	0.752
V1	1	0.942	0.005*	0.961	0.227	1	0.999
V2	0.227	1	0.059	0.92	0.824	0.424	0.847
V3	1	0.665	1	0.811	0.904	1	1
V3AB	0.974	0.745	0.589	0.992	0.040*	1	0.997
IPS0–2	0.022*	0.047*	1	0.103	0.430	1	1
IPS3–4	0.028*	<0.001*	0.999	0.949	0.994	0.021*	0.999
hA	0.997	0.066	1	0.984	1	0.979	1
A1	0.433	0.468	0.678	0.979	1	1	0.910

p values are based on permutation tests using a circular log-likelihood ratio statistic. For the neural weight index w_{AV}, they are corrected for multiple comparisons across the eight regions of interest. n = 5. Asterisks indicate significant p values. VR, visual reliability; TR, task relevance; S, spatial disparity. See also Tables S2 and S3.

control analyses. First, we evaluated participants' eye movements based on eye-tracking data recorded concurrently during fMRI acquisition. Fixation was well maintained throughout the experiment with post-stimulus saccades detected in only 2.293% ± 1.043% (mean ± SEM) of the trials. Moreover, four (visual location) × four (auditory location) × two (visual reliability) × two (task relevance) repeated measures ANOVAs performed separately for (1) % saccades or (2) % eye blinks revealed no significant main effects or interactions (Table S2). The repeated measures ANOVA on post-stimulus mean horizontal eye position (0–875 ms post-stimulus onset) revealed no significant effects either. Small trends were observed for the main effect of task relevance and visual local positions.

As a further control analysis, we therefore re-performed the linear regression analyses to compute the neural weight index w_{AV} (with fMRI-decoded spatial location as dependent variable; see the Supplemental Experimental Procedures) and included post-stimulus mean horizontal eye position as a nuisance covariate in addition to the true auditory and visual locations to predict the fMRI-decoded locations. This analysis basically replicated our initial results (Figure S2; Table S3).

Finally, we investigated the effect of within/across hemifield of presentation on our results (i.e., w_{AV}) by including a nuisance variable that coded whether the auditory and visual signals were presented in the same or different hemifield in the linear regression analysis (with fMRI-decoded spatial location as dependent variable). This analysis again basically replicated our initial results (Figure S2; Table S3).

DISCUSSION

This study combined psychophysics and multivariate fMRI pattern decoding to characterize how the brain integrates audiovisual signals into spatial representations along the auditory [12] and visual [13] processing hierarchies. Our results demonstrate that distinct computational principles govern audiovisual interactions in primary sensory and higher-order association areas.

Accumulating evidence has demonstrated that multisensory integration is not deferred to association cortices [17–22] but starts already at the primary, putatively unisensory level [23–28] via thalamo-cortical mechanisms [27], direct connectivity between sensory areas [29], or top-down influences from higher-order association cortices [30]. Our data also reveal bidirectional audiovisual influences at the primary cortical level. In particular, the auditory location influenced the spatial estimate encoded in primary visual cortex. In line with the spatial principle of multisensory integration [15], a concurrent auditory (resp. visual) signal attracted the spatial estimate in V1 (resp. A1) only when the two signals co-occurred close in space. In other words, spatial disparity controlled the influence of auditory signals on spatial estimates in primary visual areas. Yet, even for low spatial disparity, audiovisual influences in primary sensory areas were relatively small when compared to parietal cortices. These findings dovetail nicely with previous neurophysiological studies showing about 15% "multisensory" neurons in primary sensory areas [31] but more than 50% in classical association areas such as intraparietal or superior temporal sulci [32].

Critically, our study did not only show that multisensory interactions increased progressively along the cortical hierarchy but that they changed their computational operations from primary sensory to higher-order parietal areas. Only higher-order parietal areas (IPS0–4) integrated auditory and visual signals weighted by their reliability in line with principles of statistical optimality [1–3]. Yet, despite profound audiovisual interactions in IPS0–4, sensory signals were not fused into one unified amodal spatial representation [1, 3]. Instead, the sensory weights in IPS0–4 depended on the sensory modality that needed to be reported (cf. Figure 2B). This context-dependent weighting of the auditory and visual signals led to different spatial estimates for identical audiovisual stimuli under visual and auditory report.

Critically, spatial disparity increased this difference between the spatial estimates. When auditory and visual signals were far apart and hence likely to come from independent events, audiovisual integration was attenuated and IPS3–4 encoded predominantly the location of the task-relevant signal. Thus, IPS3–4 gracefully transitions between information integration and segregation depending on the probability of the two signals being generated by a common cause [4, 10].

A recent model-based fMRI study showed that IPS3–4 is more likely to encode spatial estimates formed by Bayesian causal inference [33] than by traditional forced fusion [1, 3] or full segregation models. Yet, the principles that drove this result remained

unclear (for further discussion, see the Supplemental Experimental Procedures). Using "model-free" multivariate decoding, the current study reveals three fundamental computational principles that determine audiovisual integration in IPS3–4: IPS3–4 integrates sensory signals weighted by (1) their bottom-up sensory reliabilities and (2) their top-down task relevance into multisensory spatial priority maps. (3) Critically, these spatial priority maps take into account the causal structure of the environment (i.e., interaction of task relevance with spatial disparity). The influence of task relevance and its interaction with spatial disparity implicate different spatial estimates for auditory and visual report in particular when the two signals are far apart, as expected under Bayesian causal inference. Yet, as we manipulated task relevance in long blocks, attention may potentially have increased the reliability of the auditory (resp. visual) signal and thereby influenced its weight in the final IPS3–4 spatial estimate for visual (resp. auditory) report [34]. Future studies manipulating task relevance in a cuing paradigm may help to further disentangle these different explanatory mechanisms.

Collectively, these computational operations enable IPS3–4 to form multisensory spatial priority maps that go functionally beyond traditional unisensory spatial priority maps [35, 36]. Multisensory spatial priority maps define attentional priority in space jointly based on the bottom-up salience and reliability of signals from multiple sensory modalities [22], their current task relevance, and their causal structure.

Indeed, the behavioral relevance of the IPS3–4 spatial estimates was further indicated by the correlation between the neural and behavioral weights, which progressively increased along the auditory and visual processing hierarchies to culminate in IPS3–4 [22, 37]. Likewise, IPS3–4 was the only region where perceptual report was decoded significantly better than chance.

Previous studies focusing selectively on the auditory ventriloquist illusion have highlighted the importance of the planum temporale in audiovisual integration at the perceptual level [21, 38]. Indeed, our study also revealed a high correlation between neural and behavioral weights indices in higher auditory areas. Yet, unlike IPS3–4, higher auditory areas integrated sensory signals weighted by their task relevance but were not significantly affected by visual reliability. As null results need to be interpreted with caution, future studies are needed to further define the computational similarities and differences of the planum temporale and IPS3–4 in audiovisual integration (for further discussion, see the Supplemental Experimental Procedures).

In conclusion, our results reveal distinct computational principles governing multisensory interactions in primary and association cortices. In primary visual cortices, spatial disparity controlled the influence of *non-visual signals* on the formation of spatial estimates. In parietal cortices, it determined the influence of *task-irrelevant signals*. Critically, parietal cortices integrated signals weighted by their bottom-up sensory reliabilities and top-down task relevance into multisensory spatial priority maps guiding spatial orienting and effective interactions in a multisensory world. Moving beyond identifying multisensory influences toward characterizing their computational principles reveals a hierarchical organization of multisensory perception in human neocortex. Our results demonstrate that multisensory interactions are pervasive in human neocortex but subserve distinct computational tasks [5, 39].

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and three tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.12.056.

AUTHOR CONTRIBUTIONS

T.R. and U.N. conceived and designed the experiments. T.R. performed the experiments. T.R. and U.N. analyzed the data. T.R. and U.N. wrote the paper.

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